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Brianna J. Graff
South Dakota State University

Daniel J. Dembkowski
South Dakota State University

Melissa R. Wuellner
South Dakota State University

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Phenology of Annulus Formation in Walleye and Smallmouth Bass Otoliths

Brianna J. Graff, Daniel J. Dembkowski* and Melissa R. Wuellner

Department of Natural Resource Management, South Dakota State University, Box 2140B, Brookings, SD 57007, USA

Abstract: Walleye *Sander vitreus* and smallmouth bass *Micropterus dolomieu* were sampled monthly (May-October) from Lake Sharpe, South Dakota during 2006 and 2007 to estimate the timing of otolith annulus formation and to evaluate the influence of fish age, sex, and sample location (walleye only) on the timing and detection of annulus formation. Timing of annulus formation was evaluated using marginal increment analysis. Walleye samples were stratified by age, sex, and sample location (i.e., upper and lower Lake Sharpe) and smallmouth bass samples were stratified by age and sex. Monthly mean marginal increment measurements for both species generally increased from May to June, declined in July, and slowly increased from August to October. Although monthly differences in marginal increment measurements across analysis strata were rarely consistent, July generally had the lowest mean marginal increment across species and strata, suggesting that annulus formation in walleye and smallmouth bass in Lake Sharpe likely occurs in July. The lack of differences in timing of annulus formation across species-specific strata was surprising given the well-known influences of age, sex, and water temperature on somatic growth. Nonetheless, results will aid managers in improving the accuracy of age estimates.

Keywords: Age, growth, marginal increment analysis, otolith, smallmouth bass, walleye.

INTRODUCTION

Accurate and unbiased age determination is critical in fisheries stock assessment [1]. Age information is needed to calculate growth rates, assess annual recruitment, and estimate mortality rates [2, 3]. Accurate age assignment is of particular importance for intensively managed populations of recreational fishes such as walleye *Sander vitreus* and smallmouth bass *Micropterus dolomieu*, where management strategies are designed and implemented based on estimation of growth, recruitment, and mortality.

Current methods used to estimate ages of fishes include comparison of sampled fish to known-age fish, evaluation of length-frequency distributions, and interpretation of calcified structures such as scales and otoliths [3]. For many species, otoliths have consistently provided the most accurate and precise age determinations over a broad range of ages [4-6]. Furthermore, otolith preparation and enumeration of annual growth increments (i.e., annuli) are relatively simple compared to other methods. Annuli are presumably deposited on the otolith annually during the period of greatest physiological stress, and detection of annuli is dependent upon the resumption of somatic growth. Timing of annulus deposition may be variable and is likely influenced by multiple factors [7, 8]. In northern latitudes, the period of greatest physiological stress is presumably associated with the overwinter period or with springtime and early-summer spawning; however, specific phenology of annulus formation is undocumented for a large number of species and may vary within and between individuals within a population or between populations based on intrinsic and local extrinsic characteristics (e.g., age, sex, and temperature).

Because annulus formation may occur during different times of the year, timing of sampling may influence the accuracy of age assignment if the timing of annulus formation is not known [6]. The primary objective of this study was to estimate the timing of otolith annulus formation for two walleye subpopulations and one smallmouth bass population within a mainstem Missouri River reservoir. A secondary objective was to estimate the influence of fish age, sex, and sample location (walleye only) on timing and detection of annulus formation in the same walleye and smallmouth bass populations. Annulus formation was expected to be earlier for younger fish and for females of both species due to previously documented differences in somatic growth rates among ages and between sexes [e.g., 9-11]. Given the differing thermal conditions of upper versus lower Lake Sharpe (i.e., upper Lake Sharpe receives hypolimnetic outflow from an upstream reservoir and thus has lower water temperatures), annulus formation in walleye collected from lower reaches was expected to be complete earlier than walleye collected from upper reaches.

MATERIALS AND METHODOLOGY

Walleye and smallmouth bass were sampled monthly (May – October) in 2006 and 2007 using graded-mesh gill nets (47.5-m long by 1.8-m deep with one 7.6-m panel each of 19-, 25-, 32-, 38-, 51-, and 64-mm bar mesh monofilament netting) from Lake Sharpe, South Dakota (a mainstem Missouri River reservoir). Lake Sharpe extends from Oahe Dam downstream to Big Bend Dam and has a surface area of approximately 25,000 ha (Fig. **1**). Lake Sharpe was divided into two primary sampling reaches; the upper reaches encompassed the Oahe Dam tailrace downstream to Fort

*Address correspondence to this author at the Department of Natural Resource Management, South Dakota State University, Box 2140B, Brookings, SD 57007, USA; Tel: 605 688 6577;
Email: daniel.dembkowski@sdstate.edu

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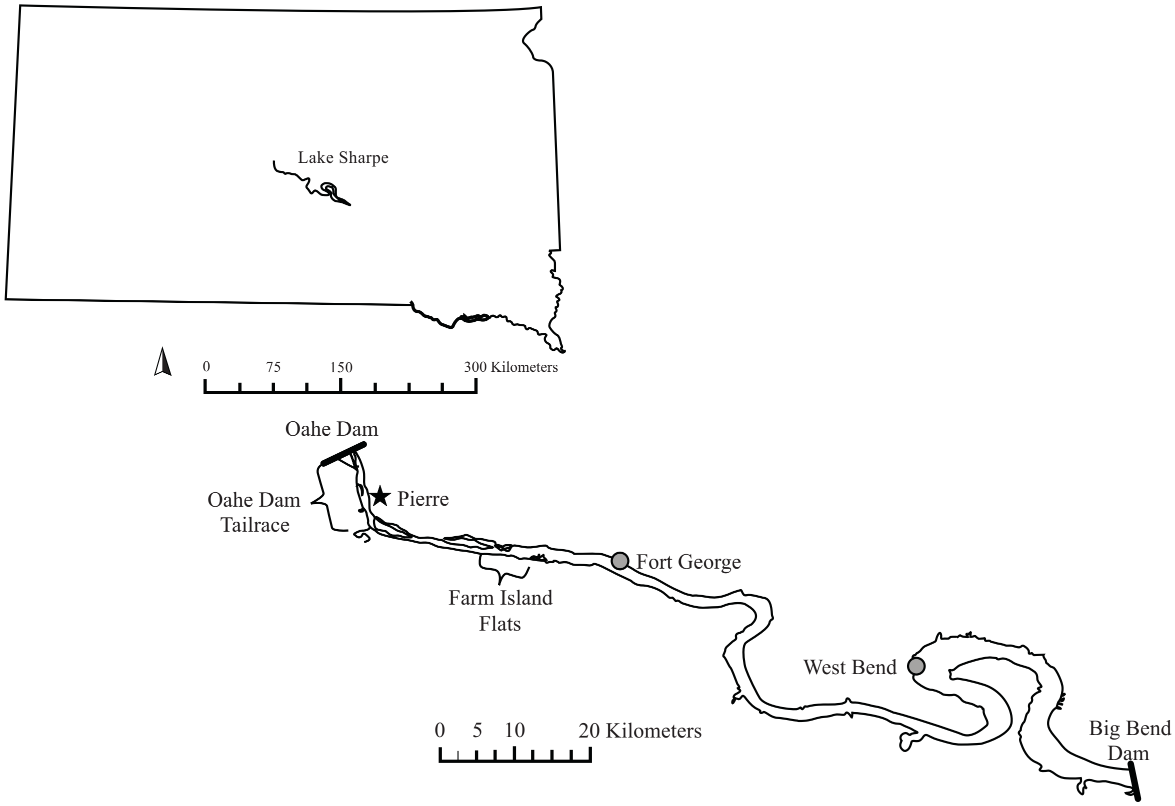

Fig. (1). Map of Lake Sharpe, South Dakota, showing the upper (Oahe Dam tailrace downstream to Fort George) and lower reaches (West Bend to Big Bend Dam). Walleye were sampled from upper and lower reaches whereas smallmouth bass were sampled only from lower reaches.

George whereas the lower reaches encompassed the area from West Bend to the Big Bend Dam (Fig. **1**). Upper reaches of Lake Sharpe receive hypolimnetic discharge from Oahe Dam. Thus, mean water temperature in the upper reaches is approximately 2°C less than mean water temperature in the lower reaches [12]. Walleye were collected from both upper and lower reaches of Lake Sharpe, whereas smallmouth bass were only collected from lower reaches (Fig. **1**). Gill net catches of walleye from the upper reaches of Lake Sharpe were supplemented with nighttime electrofishing. Sagittal otoliths were removed from each fish for age estimation.

Upon removal, otoliths were wiped clean, stored in individually labeled vials, and transported to a laboratory at South Dakota State University. Otoliths were mounted convex side down in a plastic mold (Thermo Fisher Scientific, Waltham, MA) and were embedded in epoxy (Buehler, Lake Bluff, IL; Epoxicure resin and hardener) to form a block for sectioning. Otoliths were sectioned into 0.2-mm thick sections encompassing the focus using a low-speed saw (Buehler, Lake Bluff, IL; IsoMet Model 11-1180). Sections were briefly examined under a dissecting microscope following each cut and in the instance that the first section did not include the focus, a second section was taken and the first was discarded. After sectioning, sections were lightly polished using wetted 1,200-grit silicon carbide sandpaper and placed into labeled vials.

Walleye and smallmouth bass ages were estimated by viewing otolith sections under a binocular dissecting microscope with transmitted light. The binocular dissecting microscope was fitted with an Olympus OP2-BSW camera and visual imaging software package (Olympus America, Inc., Center Valley, PA). Otolith sections were submersed in immersion oil to improve contrast between opaque and translucent bands and were viewed at 4-10X magnification depending on otolith size. Annuli were counted as the number of opaque bands and ages were estimated by a single experienced reader.

Timing of annulus formation was estimated using marginal increment analysis [13]. The marginal increment was measured as the translucent zone beyond the last complete annulus edge (Fig. **2**) [14]. An annulus was considered to be recently formed when the monthly mean marginal increment was lowest [13, 15]. Marginal increments were measured to the nearest 0.001 mm using measurement tools available in the visual imaging software program. All marginal increment measurements were made along the same trajectory (i.e., ventral anterior plane extending on the otolith rostrum; Fig. **2**) [6].

Prior to analysis, the walleye sample was stratified by sex, age, and sample location (i.e., upper and lower reaches of Lake Sharpe) and the smallmouth bass sample was stratified by sex and age. Species- and strata-specific differences in marginal increment measurements were evaluated using an analysis of variance (ANOVA), testing for differences ($P< 0.05$) in the main effects (i.e., sex, age, sample location, and month) and in the interactions among those terms. Analyses were performed with walleye and smallmouth bass

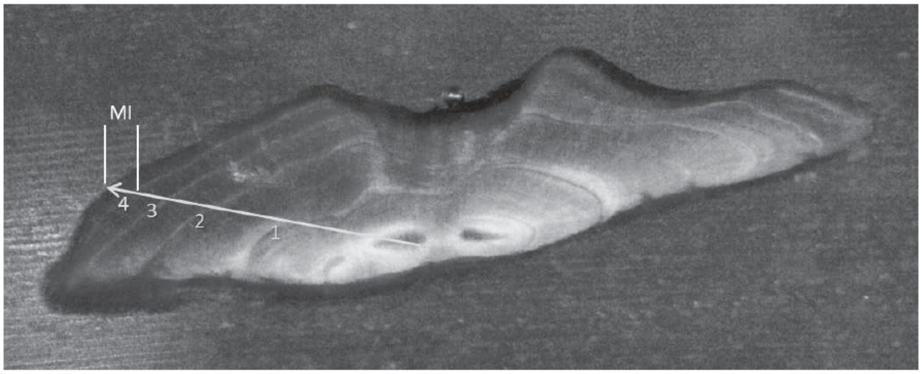

Fig. (2). Transverse cross-section of an age-4 walleye collected from upper Lake Sharpe in October 2007. The arrow depicts the plane where marginal increment (MI) measurements were made. Marginal increments were measured as the translucent zone beyond the last complete annulus edge.

samples from both years combined. All statistical analyses were performed using the Statistical Analysis System software package [16].

RESULTS

A total of 231 walleye and 271 smallmouth bass were used for analysis. Opaque and translucent bands were visible on all otoliths and estimated ages ranged 1-14 and 1-9 for walleye and smallmouth bass, respectively. Only walleye and smallmouth bass ages 2-6 were retained for analyses due to insufficient sample sizes for other cohorts.

Monthly marginal increment measurements for both walleye and smallmouth bass generally followed a "saw-toothed pattern" [*sensu* 13], with the lowest mean marginal increment occurring in summer. Marginal increments generally increased from May to June, decreased in July, and gradually increased again from August to October (Table **2**; Table **3**; Fig. **3**; Fig. **4**).

Marginal increment measurements for walleye were variable across months within age, sex, and sample location strata (Table **1**). Significant age × month interactions suggest that while marginal increment measurements differed among months, the differences were not consistent among cohorts (Table **2**; Fig. **3**, top panel). Similarly, significant sex × month and sample location × month interactions suggest that marginal increment measurements differed among months but that the differences were not consistent between males and females or walleye sampled from upper or lower Lake Sharpe, (Table **2**; Fig. **3**, middle and bottom panels). July tended to have the lowest mean marginal increment across all analysis strata (Table **2**; Fig. **3**).

Marginal increment measurements were also variable across months within age and sex strata for smallmouth bass (Table **1**). Similar to that observed for walleye, significant age × month interactions suggest that while marginal increment measurements differed among months, the differences were not consistent among cohorts. July tended to have the lowest mean marginal increment across months (Table **3**; Fig. **4**, top panel). A significant difference in marginal increment measurements was observed among months, but not between sexes or the sex × month interaction, suggesting that differences in marginal increments among months were similar for both male and female smallmouth bass (Table **1**; Table **3**; Fig. **4**, bottom panel). July tended to have the lowest mean marginal increment, but this difference was not significant (Table **3**; Fig. **4**).

Table 1. Results of ANOVAs examining marginal increment measurements relative to walleye and smallmouth bass age, sex, sample location (walleye only), and month. Results were considered significant if *P*< 0.05.

Variance source	df	*F*	*P*
Walleye			
Age			
Age	4	53.1	< 0.01
Month	5	13.5	< 0.01
Age × month	20	3.1	< 0.01
Sex			
Sex	1	0.1	0.97
Month	5	17.8	< 0.01
Sex × month	5	6.5	< 0.01
Location			
Location	1	0.1	0.73
Month	5	8.2	< 0.01
Location × month	5	5.3	< 0.01
Smallmouth bass			
Age			
Age	4	48.9	< 0.01
Month	5	18.8	< 0.01
Age × month	20	4.8	< 0.01
Sex			
Sex	1	2.2	0.14
Month	5	8.6	< 0.01
Sex × month	5	1.59	0.18

Table 2. Monthly mean marginal increment measurements for walleye sampled from Lake Sharpe, SD, in 2006 and 2007. 'Upper' and 'lower' refer to different sampling locations on upper and lower Lake Sharpe. Numbers in parentheses represent one standard error of the mean. Blank cells indicate that no fish within a given stratum were sampled that month.

	Monthly mean marginal increments (mm)					
Strata	**May**	**June**	**July**	**August**	**September**	**October**
Sex						
M	0.065 (0.004)	0.079 (0.008)	0.041 (0.003)	0.131 (0.006)	0.058 (0.005)	0.067 (0.005)
	N = 25	N = 17	N = 21	N = 2	N = 13	N = 17
F	0.112 (0.007)	0.093 (0.007)	0.046 (0.003)	0.063 (0.004)	0.066 (0.005)	0.062 (0.005)
	N = 16	N = 31	N = 16	N = 35	N = 22	N = 17
Age						
2	0.114 (0.005)	0.128 (0.007)	0.056 (0.004)	0.080 (0.005)	0.075 (0.004)	0.080 (0.007)
	N = 17	N = 14	N = 9	N = 20	N = 21	N = 10
3	0.072 (0.005)	0.092 (0.007)	0.046 (0.005)	0.051 (0.006)	0.049 (0.012)	0.070 (0.003)
	N = 8	N = 15	N = 6	N = 6	N = 3	N = 7
4	0.067 (0.010)	0.067 (0.006)	0.039 (0.002)	0.043 (0.001)	0.047 (0.003)	0.058 (0.007)
	N = 5	N = 12	N = 11	N = 3	N = 6	N = 8
5	0.053 (0.004)	0.040 (0.008)	0.030 (0.002)	0.045 (0.005)	0.044 (0.002)	0.052 (0.003)
	N = 9	N = 3	N = 5	N = 4	N = 3	N = 3
6	0.046 (0.002)	0.036 (0.003)	0.037 (0.004)	0.039 (0.005)	0.034 (0.002)	0.045 (0.004)
	N = 2	N = 4	N = 6	N = 3	N = 2	N = 6
Location						
Upper		0.067 (0.007)	0.046 (0.003)	0.054 (0.004)	0.067 (0.004)	0.070 (0.005)
		N = 9	N = 21	N = 20	N = 29	N = 20
Lower	0.107 (0.006)	0.010 (0.008)	0.043 (0.008)	0.078 (0.006)	0.045 (0.001)	0.049 (0.005)
	N = 21	N = 25	N = 2	N = 16	N = 2	N = 8

DISCUSSION

The lowest mean marginal increment across all species and strata generally occurred in July, suggesting that annulus formation in walleye and smallmouth bass in Lake Sharpe likely occurs in July. Results for walleye were inconsistent with other studies that report annulus formation in late May [17]; however, this study only included juvenile fish (age-0 and age-1) and thus is not directly comparable to ours. Results for smallmouth bass were consistent with the findings of Latta [18], who reported that annulus formation was complete during June and July for a population of smallmouth bass in Lake Michigan. Overall results are consistent with findings for yellow perch *Perca flavescens* in northeasten South Dakota glacial lakes [6]. Hales and Belk [19] and Schramm [20] found that annulus formation in bluegill *Lepomis macrochirus* may begin as early as February in the southeastern U.S. but that all individuals examined had completed annulus formation by June.

Formation of annuli is ultimately dependent upon the resumption of somatic growth following a period of slow or arrested growth (i.e., the annual period of greatest physiological stress). Differences in somatic growth rates of fish of different ages, sexes, and subject to different thermal regimes (i.e., upper versus lower Lake Sharpe, in this case), are well-documented. For example, faster somatic growth of younger cohorts compared to older cohorts has been reported for many species; a greater proportion of energetic resources are allocated to gonadal development upon sexual maturity, thus slowing somatic growth of older (i.e., sexually mature) fish [21, 22]. In the context of annulus formation, younger smallmouth bass were found to form annuli earlier in the growing season than older conspecifics in Ohio rivers [23]. Sexually dimorphic growth patterns have been demonstrated for both walleye [10] and smallmouth bass [9], with females of both species exhibiting faster growth and attaining larger sizes. Further, somatic growth is positively related to water temperature [e.g., 24, 25]. Previous research demonstrated

Table 3. Monthly mean marginal increment measurements for smallmouth bass sampled from Lake Sharpe, SD, in 2006 and 2007. Numbers in parentheses represent one standard error of the mean. Blank cells indicate that no fish within a given stratum were sampled that month.

	Monthly mean marginal increments (mm)					
Strata	**May**	**June**	**July**	**August**	**September**	**October**
Sex						
M		0.109 (0.019)	0.060 (0.011)	0.056 (0.004)	0.066 (0.005)	0.073 (0.006)
		N = 9	N = 6	N = 16	N = 24	N = 25
F	0.079 (0.005)	0.083 (0.008)	0.042 (0.002)	0.064 (0.004)	0.075 (0.006)	0.068 (0.005)
	N = 46	N = 36	N = 38	N = 32	N = 23	N = 16
Age						
2	0.131 (0.019)	0.151 (0.009)	0.050 (0.006)	0.072 (0.008)	0.086 (0.007)	0.099 (0.006)
	N = 5	N = 13	N = 14	N = 11	N = 15	N = 14
3	0.097 (0.010)	0.091 (0.013)	0.039 (0.005)	0.056 (0.005)	0.079 (0.008)	0.076 (0.005)
	N = 3	N = 2	N = 2	N = 12	N = 5	N = 4
4	0.088 (0.009)	0.053 (0.009)	0.043 (0.003)	0.050 (0.003)	0.065 (0.004)	0.071 (0.005)
	N = 15	N = 12	N = 10	N = 12	N = 6	N = 10
5	0.058 (0.007)	0.072 (0.004)	0.034 (0.003)	0.056 (0.006)	0.057 (0.006)	0.049 (0.004)
	N = 10	N = 7	N = 9	N = 7	N = 7	N = 6
6	0.058 (0.007)	0.061 (0.006)	0.036 (0.002)	0.057 (0.006)	0.049 (0.003)	0.046 (0.006)
	N = 13	N = 11	N = 9	N = 6	N = 14	N = 5

that walleye collected from the warmer lower reaches of Lake Sharpe experienced faster growth rates (i.e., greater length-at-age) than of those collected from the cooler upper reaches of Lake Sharpe [12]. Thus, differences in rates of somatic growth were expected to translate into differences in timing of otolith annulus formation. Presumably, younger fish, females, and fish subject to warmer water temperatures within their optimal thermal range would resume somatic growth earlier and thus form annuli earlier in the growing season. Nonetheless, our results suggest that timing of annulus formation was not influenced by fish age, sex, or sample location.

Several factors may have contributed to the observed lack of differences in timing of otolith annulus formation relative to fish age, sex, and sample location. It is possible that growth rates of walleye and smallmouth bass were fast enough that all cohorts included in analysis (i.e., ages 2-6) had reached sexual maturity, and thus all experienced similar increases in gonadal development at the expense of somatic growth. Both walleye and smallmouth bass typically reach sexual maturity between the ages of 2 and 4 [26-28].

Differences in the timing of annulus formation were expected between male and female smallmouth bass, largely because of the behavioral differences following spawning. After spawning, male smallmouth bass typically defend the larval and early-fry stages of their offspring for a period of 10-15 days during which they do not feed, whereas female bass typically resume normal locomotory and feeding behaviors immediately [29, 30]. Compensatory growth of male smallmouth bass may explain why a difference in timing of annulus formation was not detected between male and female bass. Compensatory growth refers to the increased growth response following a period of food shortage or reproductive loss [31, 32]. Thus, growth of male smallmouth bass following nest-guarding behavior may allow somatic growth rates to "catch-up" to those of females, possibly resulting in a lack of a difference in timing of otolith formation.

Although upper reaches of Lake Sharpe receive hypolimnetic discharge from upstream Lake Oahe, mean thermal differences (i.e., ~ 2°C during May-October) between upper and lower reaches may not have been large enough to elicit a growth response between the walleye subpopulations. Additionally, walleye in the upper reaches of Lake Sharpe experienced slightly more stable water temperatures (CV of May-October water temperatures = 27% and 31% in 2006 and 2007, respectively; M. Wuellner, unpublished data) compared to walleye in the lower reaches (CV = 29% and 33% in 2006 and 2007, respectively; M. Wuellner, unpublished data), which may have inferred an energetic advantage, thus minimizing the differences in somatic growth between subpopulations. Alternatively, walleye in Lake Sharpe may function as a single large population rather than as separate upper and lower Lake Sharpe subpopulations.

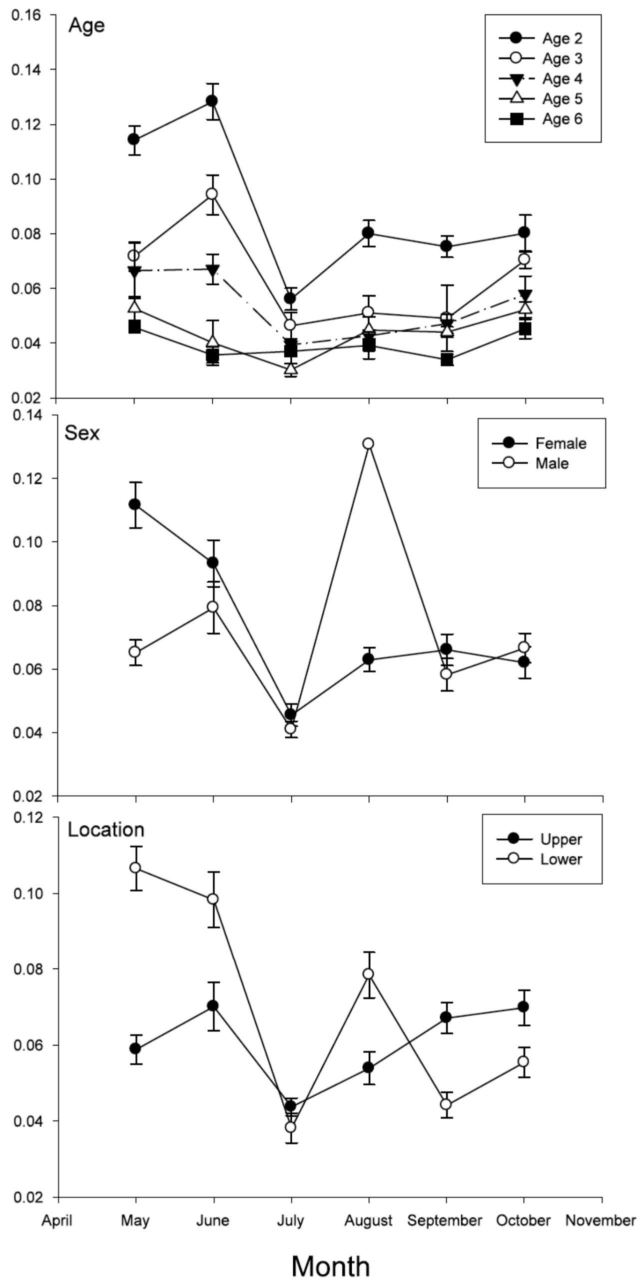

Fig. (3). Mean marginal increment distance for walleye by month across age (top panel), sex (middle panel), and sample location (bottom panel) strata. Error bars represent one standard error of the mean.

CONCLUSION

Information regarding timing of annulus formation will aid managers in improving the accuracy of age estimates, which is important for informing management decisions. Based on our findings, we recommend late-summer or fall sampling to avoid confusion related to cohort assignment stemming from variable timing of otolith annulus formation. Alternatively, if fish are sampled in late-spring or early-summer, we recommend following conventional aging methods and assigning fish ages to the next successive cohort to account for mid-summer annulus formation. While it is likely that annulus formation for walleye and smallmouth bass in Lake Sharpe occurs in July, further research including larger sample sizes among strata and greater temporal scope is needed to confirm these findings and to further examine the influence of intrinsic and extrinsic factors on the timing of otolith annulus formation.

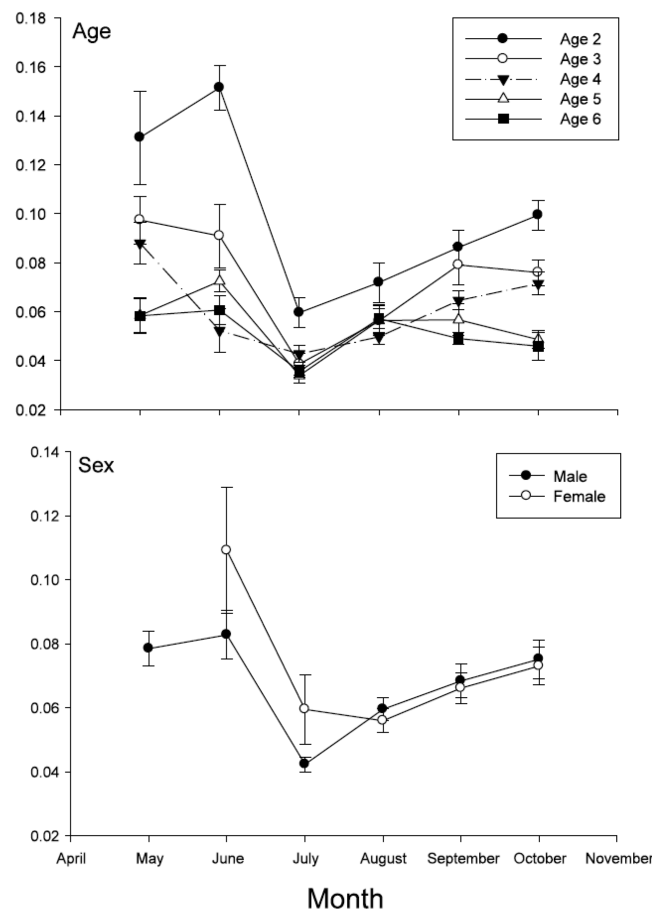

Fig. (4). Mean marginal increment distance for smallmouth bass by month across age (top panel) and sex (bottom panel) strata. Error bars represent one standard error of the mean.

CONFLICT OF INTEREST

The author(s) confirm that this article content has no conflicts of interest.

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